

Part V . Origin and Behavior of a_2^m-1

In the progeny derived from self-pollination of a plant that had undergone the chromosome type of breakage-fusion-bridge cycle in early development, an unstable expression of a gene concerned with chlorophyll development appeared. The locus responsible for this was designated ~~luteus-mutable~~ ^{in the chlorophyll complement} although the location of it was not known. During the early study of lu^m , a number of sister plants carrying it were self-pollinated. Some of these plants were C/c in constitution and a ratio of three fully pigmented to one colorless kernel was expected to appear on their ears. This ratio was found among the kernels on ears of all but one of these plants. On the ear of the exceptional plant, plant number 3908-5, in addition to fully pigmented and colorless kernels there were some kernels that had spots of deep anthocyanin pigmentation in a colorless background and the pigment type in them suggested that a gene locus resembling either A_1 or A_2 in action was responsible for this. On this ear there were 214 fully pigmented kernels, 105 totally colorless kernels, and 35 kernels that had pigmented spots in a colorless background. The pattern of variegation among the latter kernels was not alike. The majority of them had some large areas of deep pigmentation and a number of smaller spots of this. Some kernels, however, had only small spots of deep pigmentation and among them, the number of spots was not the same.

The following winter, five plants were grown from the variegated kernels on the ear just described under culture number 4062A and four plants were grown from the colorless kernels under 4062B. Four of the five plants in 4062A were self-pollinated, crossed to plants homozygous for c, and to plants carrying other gene markers. Similar tests were conducted with ^{three of the four} ^{culture} ~~the~~ plants in B of 4062. On the self-pollinated ear of the plants in 4062B, all kernels were totally colorless. Two of these plants were C/C and one was C/c. Among the four tested plants in 4062A, derived from variegated kernels, three were C/C and one was C/c (plant 4062A-1). The types of kernels that appeared on the self-pollinated ears of these plants are given in table 1. Fully pigmented kernels, ~~variegated~~ variegated kernels and colorless kernels appeared on all ears. These kernel types suggested that the gene responsible for instability of expression of anthocyanin pigmentation was undergoing mutation to give either a ~~fully~~ full expression of the gene or a null expression of it.

The following summer, plants were grown from more of the variegated kernels on the ear of plant 3908-5 and also from kernels on the ears produced by crosses of plants 4062A-3 and A-4 and 4062B-1. The variegated kernels were graded according to the pattern of pigmented spots ~~in ear~~, from those that had a number of large pigmented areas to those

~~but~~ having only a few small pigmented spots. The plants derived from the variegated kernels were themselves variegated. Note was taken of the type of this in each plant. It was obvious from these observations that some component was controlling the pattern of mutation and that this ~~was~~ component was undergoing change during plant development. Clearly defined sectors appeared in these plants in which the rate of mutation was distinctive, each sector exhibiting one particular type of this. The differences were expressed in number of ^{pigmented} ~~xxxxx~~ streaks of pigmentation and in a non-pigmented background, in the size of these streaks. These plants were tested in various ways including crosses with plants derived from the totally colorless kernels on the self-pollinated ear of plant 4062B-1 and to plants homozygous for the standard recessives of a_1 in chromosome 3, a_2 in chromosome 5, and a_3 in chromosome 10; These tests revealed that the locus responsible for the variegation expression was A_2 in chromosome 5. Some change had occurred at this locus in a cell of a plant carrying lu^m , and this was responsible for the subsequent unstable expression of ~~this~~ A_2 . The modified locus was therefore given the designation a_2^{m-1} .

Study of a_2^{m-1} was continued for several more growing seasons but from the tests of it that were made, no clear interpretation ^{was reached} ~~of its mode~~

of the mode of operation of the system responsible for control of its expression. During this period, the kernel carrying a_1^{m-1} appeared on an ear of a plant in these a_2^{m-1} cultures. Examination of its behavior, outlined in sections 2, ~~4~~ 3 and 5, made evident the system that was responsible for control of its expression. Realizing that a_1^{m-1} had arisen in a plant in which the a_2^{m-1} system was operating and that it was possible that both a_1^{m-1} and a_2^{m-1} might be controlled by the same system, study of a_2^{m-1} was recommenced in the summer of 1955. Evidence obtained during the summer of ~~1955~~ made it clear that a_2^{m-1} also was controlled by a ~~system involving~~ ^{system} a Suppressor-mutator ₁ but this Spm was ^{in the a_2^{m-1} culture} behaving in a manner distinctly different from ~~that~~ the Spm element in the a_1^{m-1} cultures. However, Some of the crosses made during the summer of 1955 indicated ^{however,} that a_2^{m-1} would respond to the Spm element ^{of} the a_1^{m-1} cultures in the same manner that a_1^{m-1} responds to it. Tests were then commenced to establish the common type of response of a_1^{m-1} and a_2^{m-1} to the Spm elements ~~that were present in the a_1^{m-1} cultures~~ and the evidence of this is reviewed in detail in part VI of this report. There is no longer any doubt that both a_1^{m-1} and a_2^{m-1} belong within the same Suppressor-mutator system. The question arises, then as to why this system was not ^{recognized} realized in the earlier study of a_2^{m-1} . There were

two main reasons for failure to recognize this. One of them involves cyclically ~~xxxxxxxx~~ exchanges in phase of action of Spm which ~~were~~ occurring in the a_2^{m-1} at times during development of the plant that obscured the recognition of ~~its~~ ^{the} presence of Spm. The other was the appearance of a state of a_2^{m-1} that differed from all other isolated states, either of a_1^{m-1} or of a_2^{m-1} . It gives rise in both plant and kernel to variegated patterns of anthocyanin pigmentation but in contrast to other states, these do not result from mutation at a_2^{m-1} . When attention was directed to the possible control of a_2^{m-1} by an Spm element, and thus, when tests to determine this were conducted, the nature of this state was quickly revealed. Subsequently, it proved to be a most important state for examining the cyclically occurring changes in phase of activity of Spm.

The early tests of a_2^{m-1} behavior and some of those conducted in 1955 and later will not be reviewed here. Nevertheless, all of them have been useful in interpreting a_2^{m-1} behavior in one way or another. Many of them illustrate change in phase of activity of Spm but until this behavior was recognized, the tests with a_2^{m-1} lacked the preciseness that is required to establish this. Therefore, in this section, only some selected tests of a_2^{m-1} will be discussed.